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On the Phylogenetic Placement of the Spider Genus *Atimiosa* Simon, 1895, and the Circumscription of *Dolichognatha* O.P.-Cambridge, 1869 (Tetragnathidae, Araneae)

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ABSTRACT

The genus *Atimiosa* Simon, 1895, is a junior synonym of *Dolichognatha* O. P.-Cambridge, 1869. This synonymy is strongly supported by cladistic analyses of morphological characters and examination of types of all known *Atimiosa* species. Two new combinations resulted from this nomenclatural change, *Dolichognatha comorensis* (Schmidt and Krause, 1993), new combination, and *Dolichognatha quinquemucronata* (Simon, 1895), new combination. New illustrations and photographs of these two species and of the poorly known *Dolichognatha longiceps* (Thorell, 1895) are provided. We also describe for the first time the web architecture of *D. longiceps*.

INTRODUCTION

Tetragnathidae is a family of orbweaving spiders found worldwide; however, most of its

species diversity is concentrated in the humid tropical regions of the world. More than 900 valid species of tetragnathids have been described, classified in 47 genera (Platnick,

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2010). Many tetragnathid genera are associated with ecosystems neighboring freshwater bodies, such as lakes or rivers, where their population density is often very high, making them the dominating orbweavers in the habitat. Members of the family are also common in humid tropical forests where they are found from the ground level to the top of the canopy. As with many other tropical arthropods, most of the diversity is still undescribed. Inadequate descriptions and poor knowledge of many of the species further complicates any systematic work, hence the need for generic systematic revisions to address this problem. In recent years, several authors have addressed different aspects of tetragnathid systematics (e.g., Tanikawa, 2001; Gillespie, 2003a, 2003b; Álvarez-Padilla, 2007; Dimitrov et al., 2008; Smith, 2008; Dimitrov and Hormiga, 2009; Álvarez-Padilla et al., 2009), but due to the large size of the group many genera still require systematic revisions. The present paper is a continuation of our efforts to update tetragnathid systematics. It focuses on the South Asian genus *Atimiosa* Simon, 1895. We have examined the type specimens of the two known species of *Atimiosa* and studied their phylogenetic position within Tetragnathidae using morphological characters. The type species, *Atimiosa quinquemucronata* Simon, 1895, was originally described by Simon (1895) based on a subadult female specimen (fig. 1A–E) from Sri Lanka that is conspicuously similar to some *Dolichognatha* species. Schmidt and Krause (1993) subsequently described another species, *Atimiosa comorensis* Schmidt and Krause, 1993, from the Comoro Islands. It is in fact puzzling how Schmidt and Krause (1993) may have decided on this generic placement given that Simon's description mentions very few diagnostic traits, all of them consistent with *Dolichognatha*. A rationale for the generic placement is absent from Schmidt and Krause's paper. In this paper we propose the synonymization of the genus *Atimiosa* with *Dolichognatha* based on the examination of the type specimens of both species and on the results of cladistic analyses that include all known *Atimiosa* species and a broad sample of tetragnathids. Recent treatments of *Dolichognatha* and several small and poorly

known tetragnathid genera from Australasia and Africa have produced six generic synonymies for *Dolichognatha* (Levi, 1981; Smith, 2008). In addition, they have also provided illustrated descriptions of several *Dolichognatha* species. We extend these efforts to facilitate identification and future taxonomic work by providing illustrations and photographs of all species formerly included in *Atimiosa*. Specimens of the poorly known species *Dolichognatha longiceps* (Thorell, 1895) are also illustrated and included in the analyses to better test the monophyly of the genus; that species was also selected because of its unusual morphological features, such as the absence of PME. Here we provide additional illustrations of *D. longiceps* and document for the first time its web architecture.

MATERIALS AND METHODS

Type specimens for this study were borrowed from the museum collections listed at the end of this section. Specimens from *Dolichognatha longiceps* were collected by GH in Thailand. Digital photographs of the type in the Muséum National d'Histoire Naturelle, Paris (MNHN) were taken by FAP with a Nikon Coolpix 995 camera while visiting the collections. The morphological methods of our study follow those previously described in Hormiga (2002). Other specimens were examined and illustrated using Leica MZ16 or Leica MZ16A stereoscopic microscopes with a camera lucida and Leica DMRM compound microscope with a drawing tube. Drawings were prepared with graphite pencils on acid-free cotton paper. Hairs and macrosetae are not depicted in the final drawings. For male palp illustrations the left palp was used. Epigyna were treated with SIGMA Pancreatin LP 1750 enzyme complex (Álvarez-Padilla and Hormiga, 2008) and transferred to methyl salicylate solution for examination and illustration.

All pencil drawings were scanned and further improved with the help of the Gimp 2.4 and Adobe Photoshop CS2 programs. Digital images of the specimens were taken in alcohol with Nikon DXM1200F digital camera mounted on a Leica MZ16A stereoscopic microscope. Final plate layout and editing was

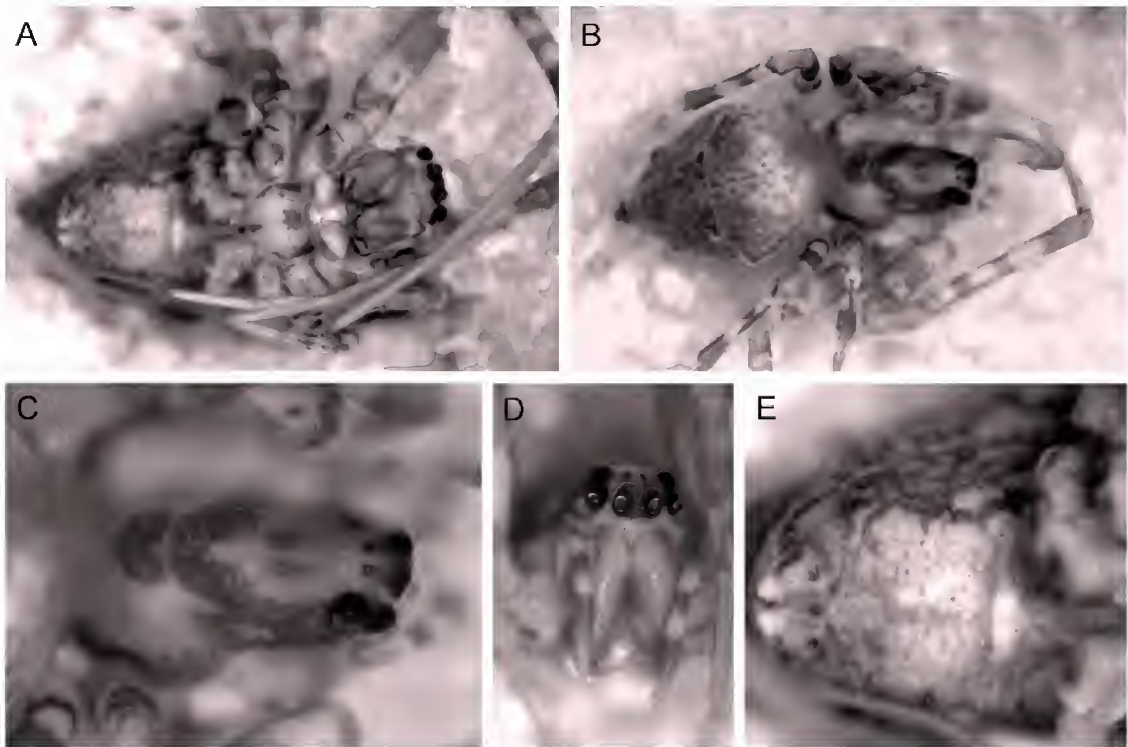


Fig. 1. *Dolichognatha quinquemucronata* (Simon, 1895), new combination. Subadult female holotype from Sri Lanka (MNHM 16140): ventral (A), dorsal (B). Cephalothorax: dorsal (C), frontal (D). Abdomen and genital area, ventral (E).

done with Adobe Illustrator CS2. All measurements are in millimeters.

ABBREVIATIONS USED IN TEXT AND FIGURES

ALE	anterior lateral eyes
C	conductor
CB	cymbium
CEBP	cymbial ecto-basal process
CD	copulatory duct
E	embolus
FD	fertilization duct
MEA	metine embolic apophysis
MPT	maximum parsimony tree
P	paracymbium
PLE	posterior lateral eyes
PME	posterior median eyes
S	spermatheca
ST	subtegulum
T	tegulum

MUSEUM COLLECTIONS

AMNH	American Museum of Natural History, New York, USA
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MCZ	Museum of Comparative Zoology, Cambridge, USA
MNHN	Muséum National d'Histoire Naturelle, Paris, France
NRM	Naturhistoriska riksmuseet, Stockholm, Sweden
RMCA	Musée royal de l'Afrique centrale, Tervuren, Belgium

PHYLOGENETICS

Morphological characters for *Atimiosa comorensis*, *A. quinquemucronata*, *Dolichognatha incaensis* (Simon, 1895), *D. longiceps*, and *Cyrtognatha insolita* (Chickering, 1956) were scored (Appendix 1) and added to the morphological matrix of Álvarez-Padilla et al. (2009). That work (Álvarez-Padilla et al., 2009) provides the largest and most complete morphological data matrix for Tetragnathidae to date, along with a large number of out-group representatives. This relatively extensive taxon sample, coupled with the large number of characters (213 morphological and behav-

ioral characters), allows robust testing of phylogenetic hypotheses for the relationships of tetragnathid genera. Here we use that dataset to test the phylogenetic position of the tetragnathid genus *Atimiosa*. We retain the original taxon sample of Álvarez-Padilla et al. (2009) and add to the matrix the taxa listed above and in Appendix 1.

Very few characters were scored for *A. quinquemucronata* because the only specimen available for study was the subadult type. Nonetheless, we have added this species to the matrix because it is the type species of the genus *Atimiosa*. Several somatic characters reflecting traits such as eye size and distribution, which do not show sexual dimorphism, were scored from the male type of *A. comorensis*. *Dolichognatha incaensis* specimens were not directly examined, but we used available information (SEM images, drawings, descriptions, and character scores) from the literature (Smith, 2008). The type species of *Dolichognatha*, *D. nietneri* O. P.-Cambridge, 1869, was not included in the analyses. This species is known from just a single male specimen lodged in the Natural History Museum (London). The original description of *D. nietneri* provides very detailed information on the somatic morphology of this species (O. P.-Cambridge, 1869). The type specimen was also examined by Levi (1981), who confirmed O.P.-Cambridge's observations. Based on these data we can confirm that *D. longiceps* and *D. incaensis* are congeneric with *D. nietneri* and that all of them share the same putative synapomorphies of the genus. The monophyly of *Dolichognatha* is not questioned, and thus, unlike in the case of *Atimiosa* whose type species is a subadult specimen with unclear affinities, we did not include *D. nietneri* in the analyses. Instead, we scored two other species (*D. longiceps* and *D. incaensis*) for which we have detailed information of male and female morphology and behavior (in the case of *D. longiceps*). *Dolichognatha pentagona* (Hentz, 1850) is the only other *Dolichognatha* species for which detailed morphological and behavioral information is available and it was already included in the matrix of Álvarez-Padilla et al. (2009). We have also added the species *C. insolita* to the analyses to better represent the morphological variability of *Cyrtognatha* (see appendix 1). The character scores of *C. insolita*

are based on direct examination of the holotype (male from Panama, Barro Colorado Island, in MCZ 21668) in addition to the SEM images, drawings, and descriptions provided by Dimitrov and Hormiga (2009). One characteristic of *C. insolita*, the presence of a "metine embolic apophysis" (MEA), is particularly relevant as most of the species of *Cyrtognatha* have this apophysis (Dimitrov and Hormiga, 2009), which is absent in *C. espanola* (Bryant, 1945). The latter species was used in the phylogenetic analyses of Álvarez-Padilla et al. (2009). *Dolichognatha* has an MEA and the proper representation of the dominant embolic morphology in *Cyrtognatha* is important for the correct optimization of this character. To reflect recent observations we have also changed two scores for *Pachygnatha autumnalis* Marx, 1884 as follows: character 154 (female abdominal dorsal surface) from 0 to 1 and character 183 (male palpal trochanter length) from 0 to 1. Character descriptions are discussed elsewhere (Dimitrov and Hormiga, 2009; Álvarez-Padilla et al., 2009). Character numbers and character definitions are as in Álvarez-Padilla et al. (2009).

Matrix editing and manipulation was performed in Mesquite version 2.0 (build i69) (Maddison and Maddison, 2008). Parsimony analyses under equal and implied weights were performed in TNT version 1.1 (Goloboff et al., 2003). Cladistic analyses were performed following the methodology of Dimitrov and Hormiga (2009).

RESULTS FROM THE CLADISTIC ANALYSES

Analysis of the complete data matrix under equal weights found six minimal length trees 1045 steps long (CI = 0.26, RI = 0.60). The strict consensus of these trees is shown in figure 9 (L = 1059, CI = 0.25, RI = 0.60). *Atimiosa comorensis* is nested in a clade together with the *Dolichognatha* species and *A. quinquemucronata*, but this clade is not well supported by resampling indices and Bremer support. The sister group of *Dolichognatha* is the genus *Metellina* Chamberlin and Ivie, 1941. *Dolichognatha* together with *Meta* C.L. Koch, 1836, and *Metellina* form a monophyletic group but it does not receive support from the resampling indices and

Bremer support is low (Bremer support = 1). When missing data are reduced by excluding *A. quinquemucronata* (92.5% missing data) from the analyses, the same six trees are found, but they are one step shorter ($L = 1044$, $CI = 0.26$, $RI = 0.60$). Their strict consensus is shown in figure 10 ($L = 1058$, $CI = 0.25$, $RI = 0.60$). The topology of these trees is exactly the same as when *A. quinquemucronata* is included in the analyses with one difference: the clade that includes the species of *Dolichognatha* and *A. comorensis* receives very high support from the resampling indices and has the highest Bremer support (12).

Analyses under implied weights always recover a monophyletic group that includes *Dolichognatha*, *Meta*, and *Metellina*. The topology of this group is the same as under equal weights when $k \geq 5$. At k values lower than 5 *Dolichognatha* (including *Atimiosa*) is paraphyletic with respect to *Meta* and *Metellina*. The same results are obtained when *A. quinquemucronata* is excluded from the analyses (fig. 11).

Three additional monophyletic groups that receive support and are stable under different analytical treatments can be distinguished within Tetragnathidae: Leucauginae, Tetragnathinae, and the Australian lineage known as “*Nanometa* clade” (see Álvarez-Padilla, 2007; Dimitrov and Hormiga, 2009; Álvarez-Padilla et al., 2009). The phylogenetic placement of the genera *Azilia* Keyserling, 1881, *Mollemeta* Álvarez-Padilla, 2007, *Chrysometa* Simon, 1894, and *Allende* Álvarez-Padilla, 2007, however, is very unstable and varies with values of k . Alternative topologies under different k values when missing data are reduced (*A. quinquemucronata* excluded from the analyses) are shown in figure 11.

Tetragnathidae is recovered as monophyletic in all analyses, but it does not receive support from any of the resampling indices. However, tetragnathids are well supported by the Bremer support (5) when missing data are reduced (fig. 10).

DISCUSSION

Our results show that if treated as a separate genus, *Atimiosa* would render *Dolichognatha*

paraphyletic. If *Atimiosa comorensis* were to be transferred to the genus *Dolichognatha*, *Atimiosa* would be rendered monotypic and sister to *Dolichognatha*, which we view as undesirable. Detailed examination of the morphology of *Atimiosa quinquemucronata* shows that it has all diagnostic characters of *Dolichognatha* (e.g., see Levi, 1981). Treating *Atimiosa* as a junior synonym of *Dolichognatha* is the soundest alternative.

Results from different analytical treatments always recovered a Metainae lineage including *Dolichognatha*, *Meta* and *Metellina*. For further discussion on higher-level tetragnathid relationships, see recent phylogenetic treatments in Álvarez-Padilla (2007), Dimitrov and Hormiga (2009), and Álvarez-Padilla et al. (2009).

A very interesting feature of *D. longiceps* that deserves comment is the strong reduction of the PME. As far as we know this is the only case in tetragnathids where complete eye reduction (loss) has taken place. Cases of eye reduction are common in cave-dwelling spiders and there are many *Meta* species known to exhibit cavernicolous tendencies. All known species of *Meta*, however, have eight eyes. Interestingly *D. longiceps* does not live in caves but in humid Southeast Asian tropical forests where it builds its webs near the ground between the roots and buttresses of trees (fig. 8). Variation in the size of the PME across *Dolichognatha* species suggests a possible process of eye reduction in this genus. The evolutionary forces driving this process and its biological significance remain unknown.

TAXONOMY

Dolichognatha O. P.-Cambridge, 1869

TYPE SPECIES: *Dolichognatha nietneri* O. P.-Cambridge, 1869.

Landana Simon, 1884, transferred from Archaeidae to Araneidae by Lehtinen, 1967: 289, here by Levi, 1981: 277.

Parebius Thorell, 1894, *Prolochus* Thorell, 1895, *Nicholasia* Bryant and Archer, 1940, type *Araneus pentagonus* (Hentz, 1850) and *Afiamalu* Marples, 1955, type *Afiamalu richardi* Marples, 1955, transferred here by Levi, 1981: 277.

Homalopolys Simon, 1895, transferred here by Smith, 2008: 10.

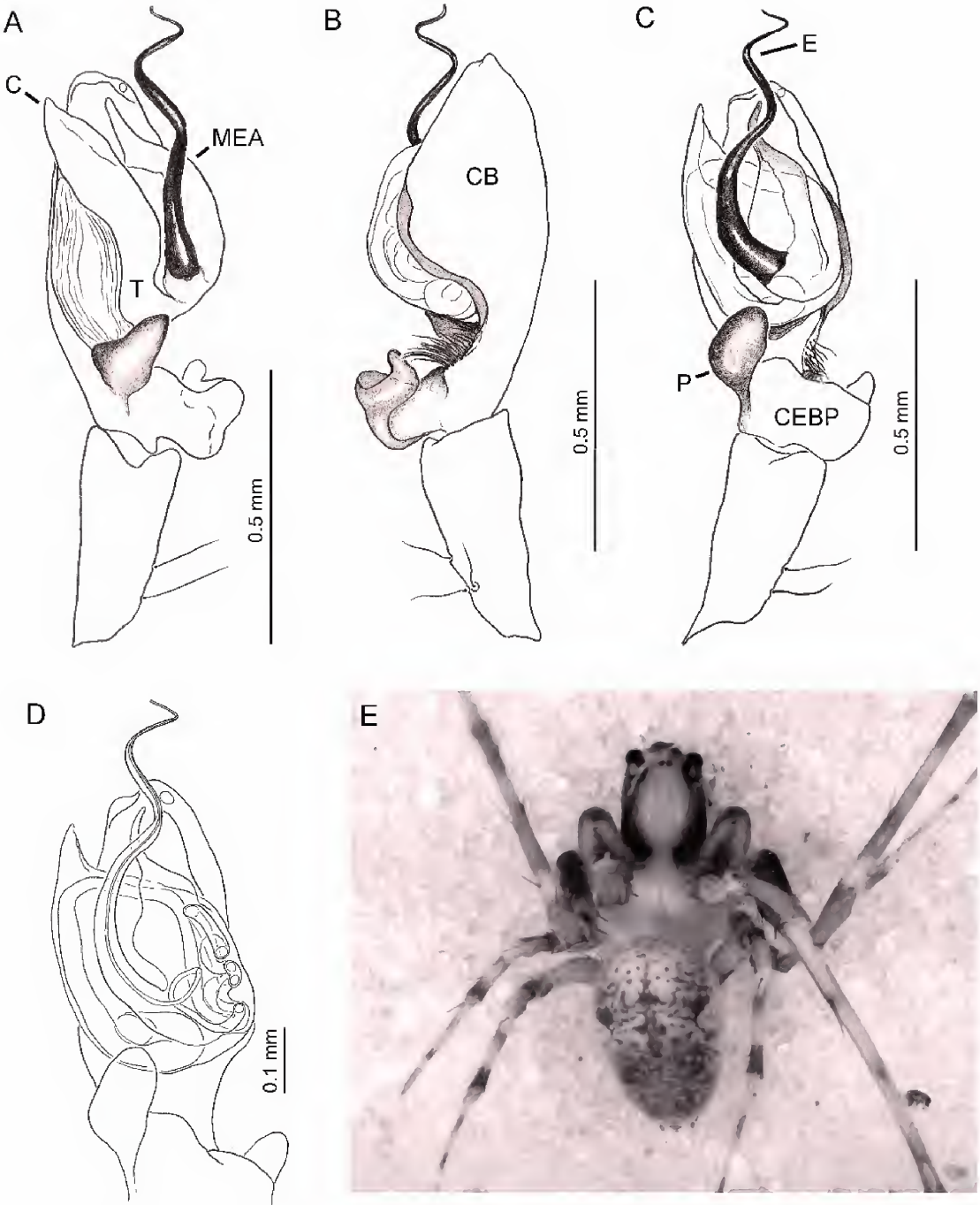


Fig. 2. *Dolichognatha comorensis* (Schmidt and Krause, 1993), new combination. Male palp: prolateral (A), retrolateral (B), ventral (C), schematic (ventral) (D). Habitus: dorsal (E).

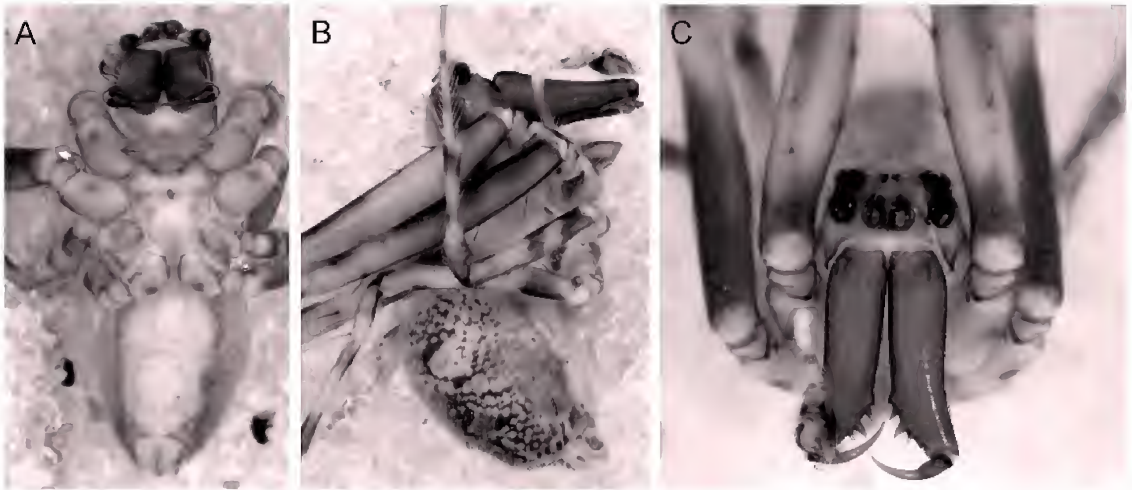


Fig. 3. *Dolichognatha comorensis* (Schmidt and Krause, 1993), new combination holotype from Grande Comoro (RMCA 160.649). Male: ventral (A), lateral (B), frontal (C).

Atimiosa Simon, 1895, **new synonymy**, type species *Atimiosa quinquemucronata* Simon, 1895.

JUSTIFICATION FOR THE SYNONYMY: The holotype of *Atimiosa quinquemucronata* is a subadult female. Describing new taxa based on juvenile specimens was common before the early 20th century. The validity of taxa based on such specimens is often difficult to assess because genital morphology cannot be examined and they are subsequently neglected or treated as nomina dubia. Fortunately, *A. quinquemucronata* shares some easily recognizable somatic features with the genus *Dolichognatha*, such as the separated lateral eyes, PME smaller than the lateral eyes, and the absence of fourth femur trichobothria in females. The size and distribution of the eyes are particularly relevant, as those are among the most important diagnostic characters of *Dolichognatha*. The pointed tip of the abdomen and the shape of the labium and sternum are also as in *Dolichognatha*. Based on these observations and the results from our cladistic analyses (figs. 9; 10), we transfer all *Atimiosa* species to *Dolichognatha*, which renders the former genus into a junior synonym of *Dolichognatha*.

DIAGNOSIS: The genus *Dolichognatha* can be most easily distinguished from close relatives (*Meta* and *Metellina*) by the very long male chelicerae and the characteristic shape

and coloration of the prosoma. In *Dolichognatha* the cephalic region is rectangular in shape and elongated with dark sides (e.g., fig. 6A). In addition, the following combination of characters differentiates *Dolichognatha* from other tetragnathids: aggregate spigots not embracing the flagelliform spigot, PME and PLE without canoe tapetum, PME smaller than PLE, abdomen with anterior tubercles, and horizontal orb web with closed web hub close to the substrate.

PHYLOGENETICS: The monophyly of *Dolichognatha* is supported by all analyses and it is placed in a Metainae lineage together with the genera *Meta* and *Metellina* (figs. 9; 10), which includes also *Mollemeta*, *Chrysometa*, and *Allende* when $k = 4-7$ (fig. 11). All analyses, except when $k \leq 3$, found *Dolichognatha* sister to *Metellina*. Three unambiguous synapomorphies support the monophyly of *Dolichognatha* (fig. 12A): PLE larger than PME, lateral eyes separated, and anterior abdominal tubercles present. When *A. quinquemucronata* is excluded from the analyses the number of synapomorphies supporting *Dolichognatha* increases to 17 (fig. 12B) due to the reduction of data missing from the matrix. These synapomorphies include: aggregate spigots not embracing the flagelliform spigot; apically distended conductor path; short clypeus; PME close to each other (less than one PME

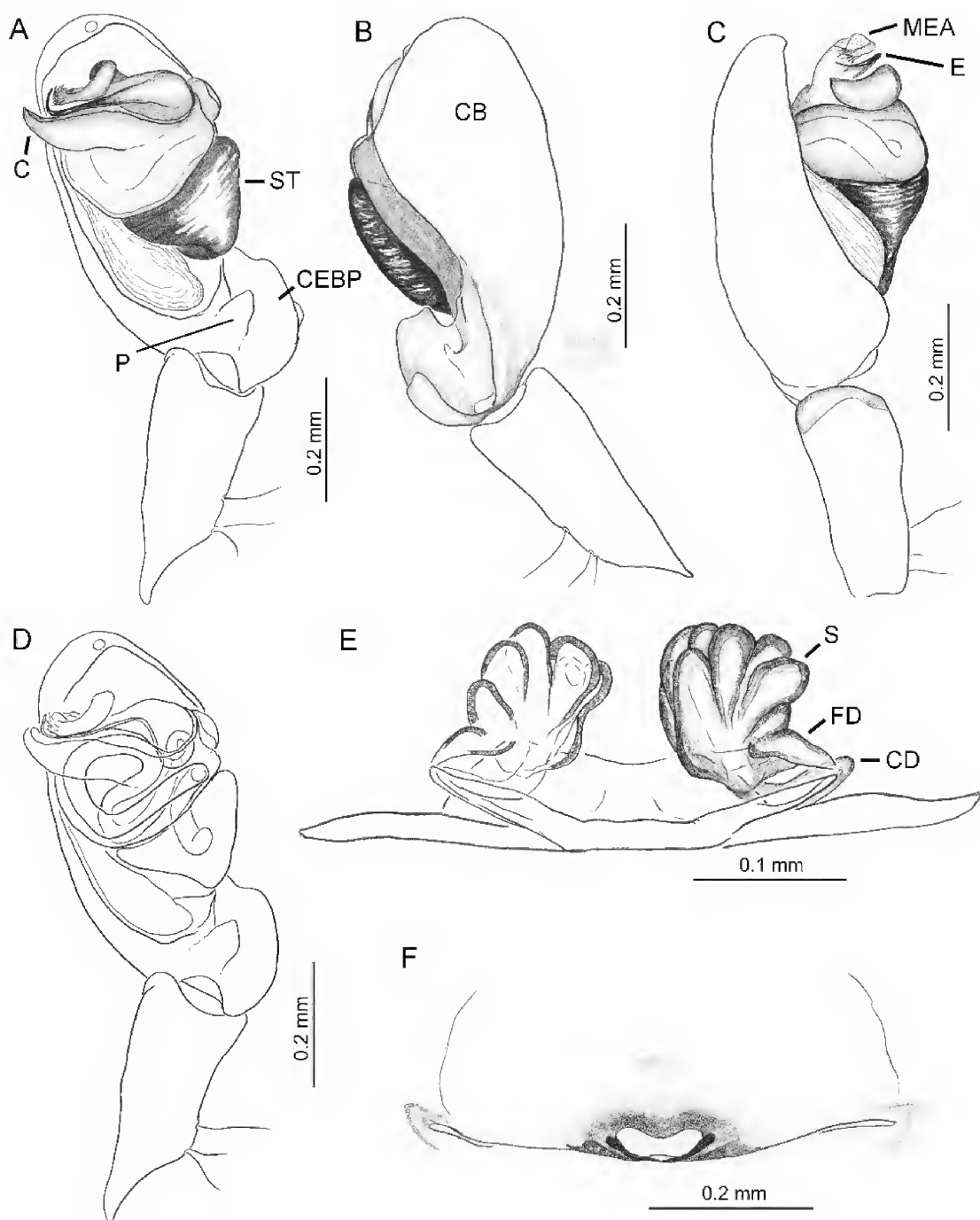


Fig. 4. *Dolichognatha longiceps* (Thorell, 1895) from Thailand (specimen in AMNH). Male palp: ventral (A), retroalateral (B), prolateral (C), schematic (ventral) (D). *Dolichognatha longiceps* (Thorell, 1895) from Thailand (specimen in AMNH). Epigynum: dorsal (E), ventral (F).

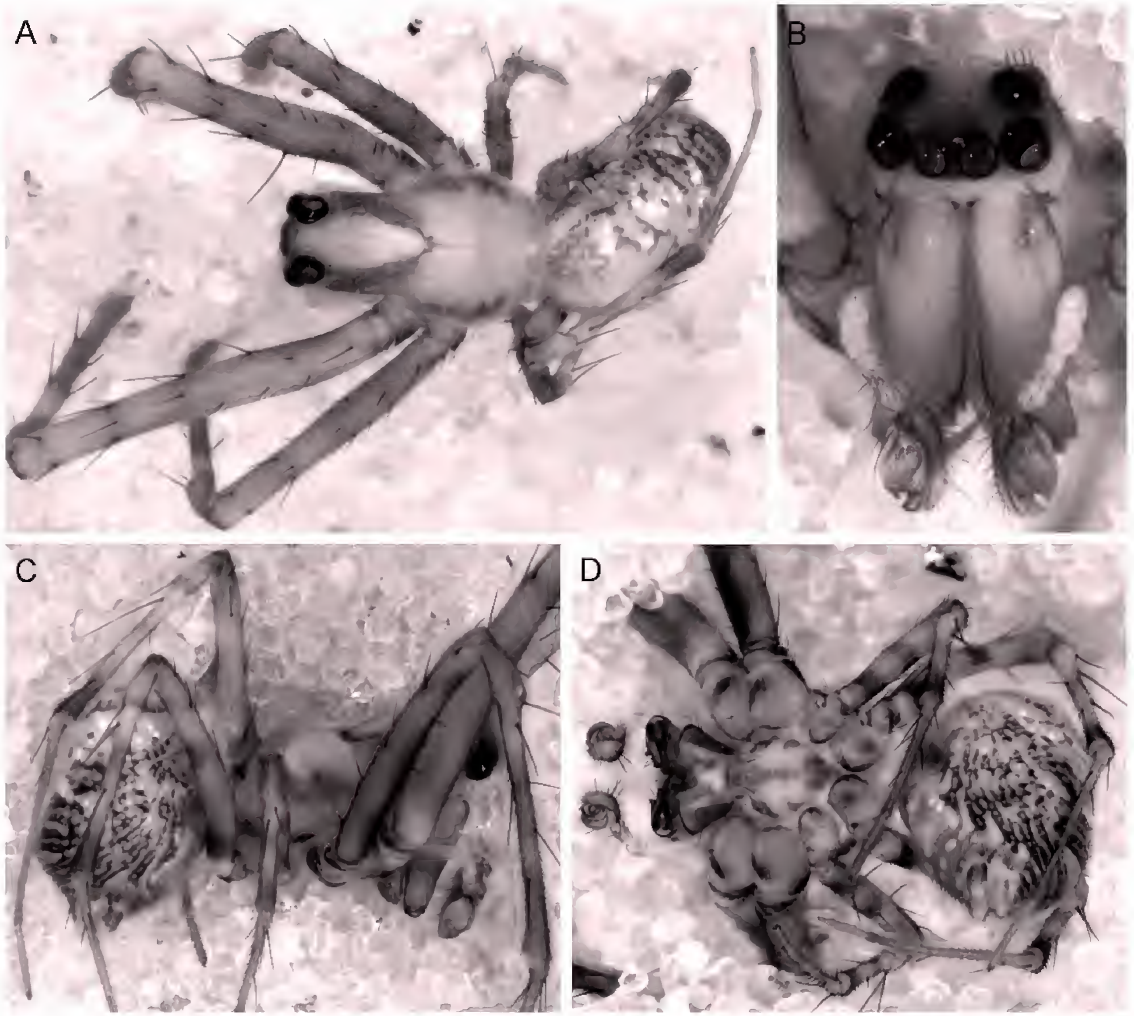


Fig. 5. *Dolichognatha longiceps* (Thorell, 1895) from Thailand (specimen in AMNH). Male: dorsal (A), frontal (B), lateral (C), ventral (D).

diameter); PME without canoe tapetum; PLE without canoe tapetum; PME smaller than PLE; lateral eyes separated; male paturon with a basal tubercle; male chelicerae larger than in female; intermediate length of copulatory ducts; short fertilization ducts; abdomen with anterior tubercles; male palpal patella without macrosetae; horizontal orb web; and closed web hub.

COMPOSITION: *Dolichognatha* comprises 29 described species (Platnick, 2010), including the two new combinations proposed here: *D. aethiopica* Tullgren, 1910; *D. albida* (Simon, 1895); *D. baforti* (Legendre, 1967); *D. cygnea*

(Simon, 1893); *D. deelemanae* Smith, 2008; *D. ducke* Lise, 1993; *D. erwini* Brescovit and Cunha, 2001; *D. incanescens*; *D. kampa* Brescovit and Cunha, 2001; *D. kratochvili* (Lessert, 1938); *D. lodiculafaciens* (Hingston, 1932); *D. longiceps*; *D. mandibularis* (Thorell, 1894); *D. mapia* Brescovit and Cunha, 2001; *D. maturaca* Lise, 1993; *D. minuscula* (Mello-Leitão, 1940); *D. nietneri*; *D. pentagona*; *D. petiti* (Simon, 1884); *D. pinheiral* Brescovit and Cunha, 2001; *D. proserpina* (Mello-Leitão, 1943); *D. quadrituberculata* (Keyserling, 1883); *D. raveni* Smith, 2008; *D. richardi* (Marples, 1955); *D. spinosa* (Petrunkévitch, 1939); *D.*

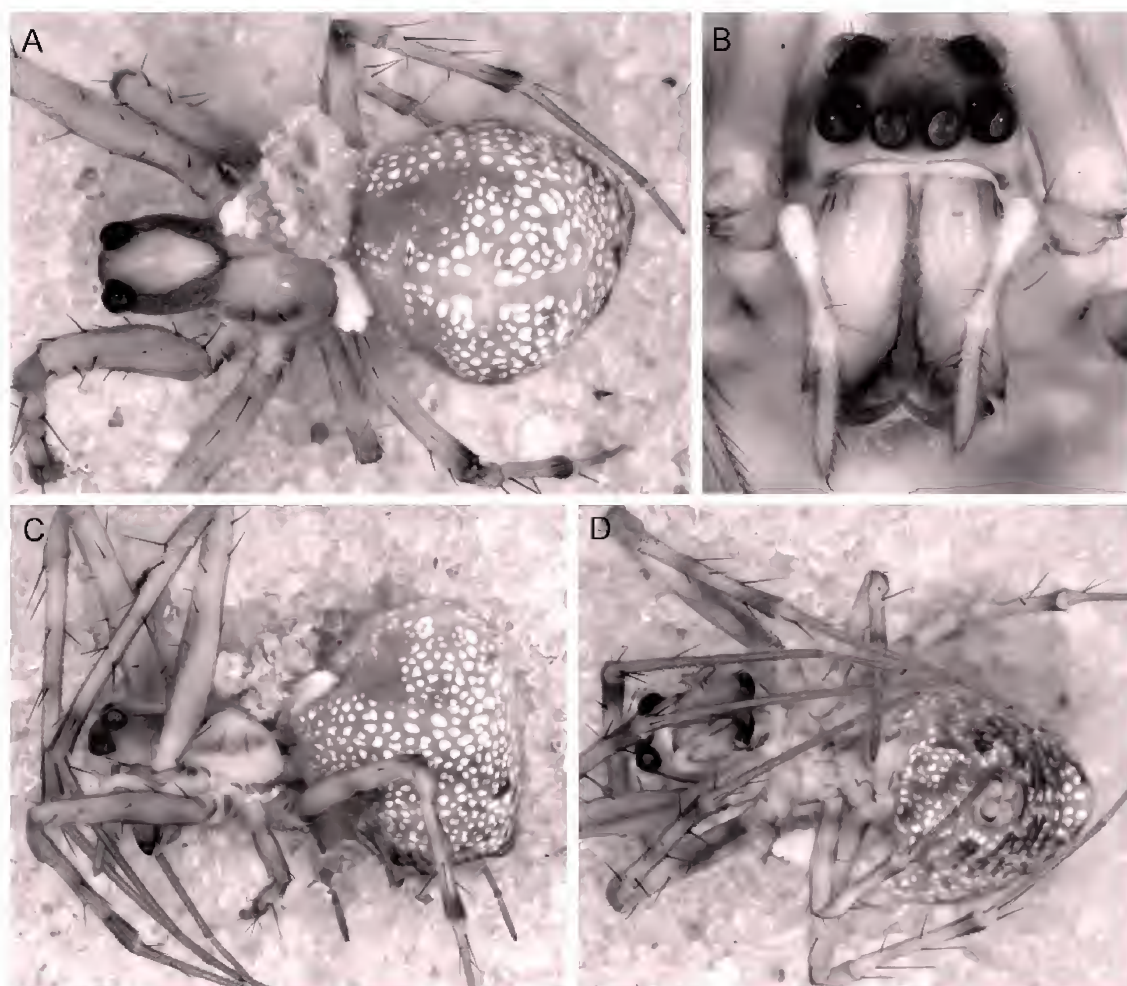


Fig. 6. *Dolichognatha longiceps* (Thorell, 1895) from Thailand (specimen in AMNH). Female: dorsal (A), frontal (B), lateral (C), ventral (D).

tigrina Simon, 1893; *D. umbrophila* Tanikawa, 1991; *D. quinquemucronata* (Simon, 1895), **new combination**; and *D. comorensis* (Schmidt and Krause, 1993), **new combination**.

DISTRIBUTION: *Dolichognatha* has a circum-tropical distribution with the highest species diversity in South America and Southeast Asia.

NATURAL HISTORY: The majority of *Dolichognatha* species live near the ground where they build nearly horizontal orb webs (Levi, 1981; Smith, 2008 and observations reported herein). However, there are at least some species, such as *D. albida*, that were reported to build vertical orb webs (Simon, 1894). Smith (2008) confirms that *Dolichognatha*



Fig. 7. *Dolichognatha longiceps* (Thorell, 1895) from Thailand (specimen in AMNH), epigynum.

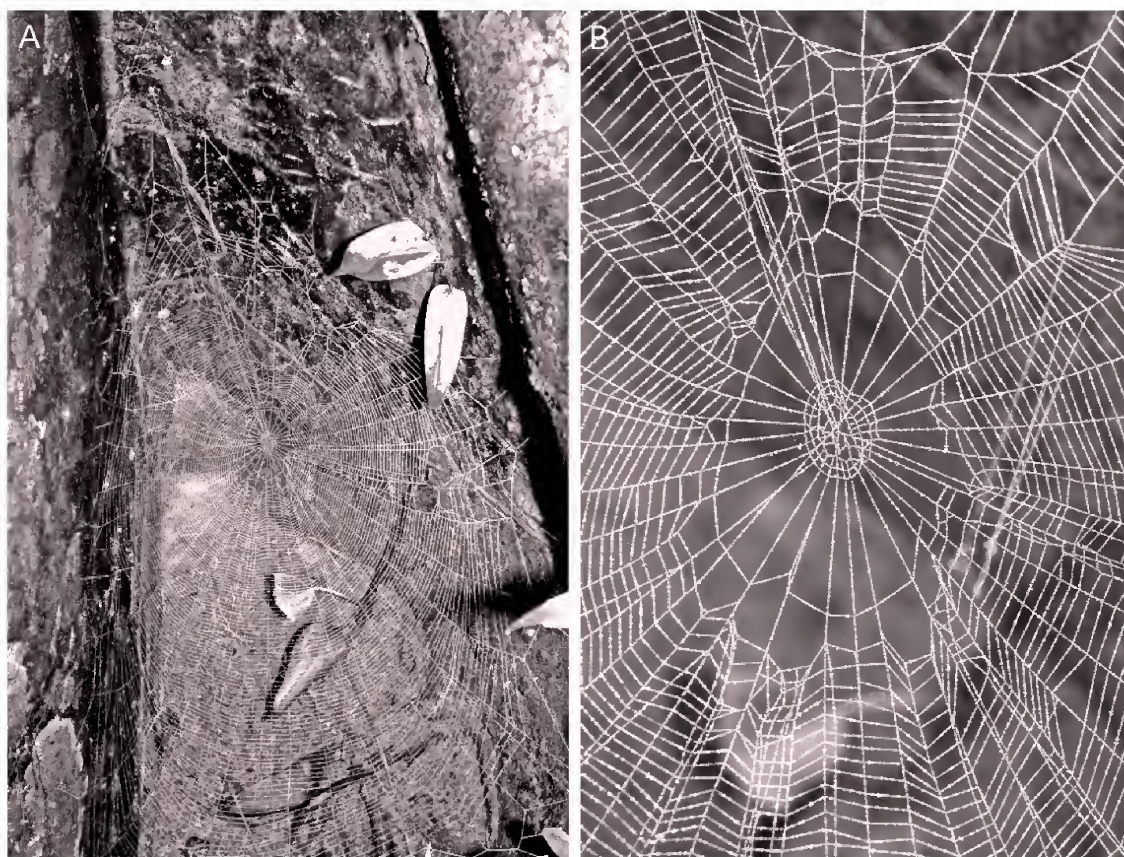


Fig. 8. *Dolichognatha longiceps* (Thorell, 1895) from Thailand. Web architecture (web about 40 cm wide; photo F. Álvarez-Padilla) (A), hub (photo F. Álvarez-Padilla) (B).

species may live in the canopy, as specimens for her study were collected using canopy-fogging techniques. Unfortunately, she did not observe the webs of these specimens. Our observations of *D. longiceps* webs are consistent with the descriptions of Levi (1981) and represent the most common web architecture in *Dolichognatha* (horizontal orbs close to the substrate).

Dolichognatha quinquemucronata (Simon, 1895), **new combination**

Figures 1A–E

Atimiosa quinquemucronata Simon, 1894: 742 (nomen nudum).

Atimiosa quinquemucronata Simon, 1895a: 154.

TYPE: Subadult female holotype from Sri Lanka. The only information on the label,

other than the collection number and the species name, is “Nuw. El.” (MNHN 16140, examined).

JUSTIFICATION OF THE TRANSFER: The type specimen, which is also the only known specimen of this species, is a subadult female (fig. 1A, E), thus it is impossible to study its genital morphology. However, it has all somatic characters diagnostic of *Dolichognatha*, such as: PME smaller than the PLE, PLE, and ALE separated, chelicerae slender and elongated, and femur IV without trichobothria. Even with 92.5% missing data in the data matrix, the cladistic analyses unambiguously placed this species in a group together with the *Dolichognatha* species included in our analyses and with *A. comorensis*. Based on this cladistic hypothesis (fig. 9), we transfer *A. quinquemucronata* to the genus *Dolichognatha*.

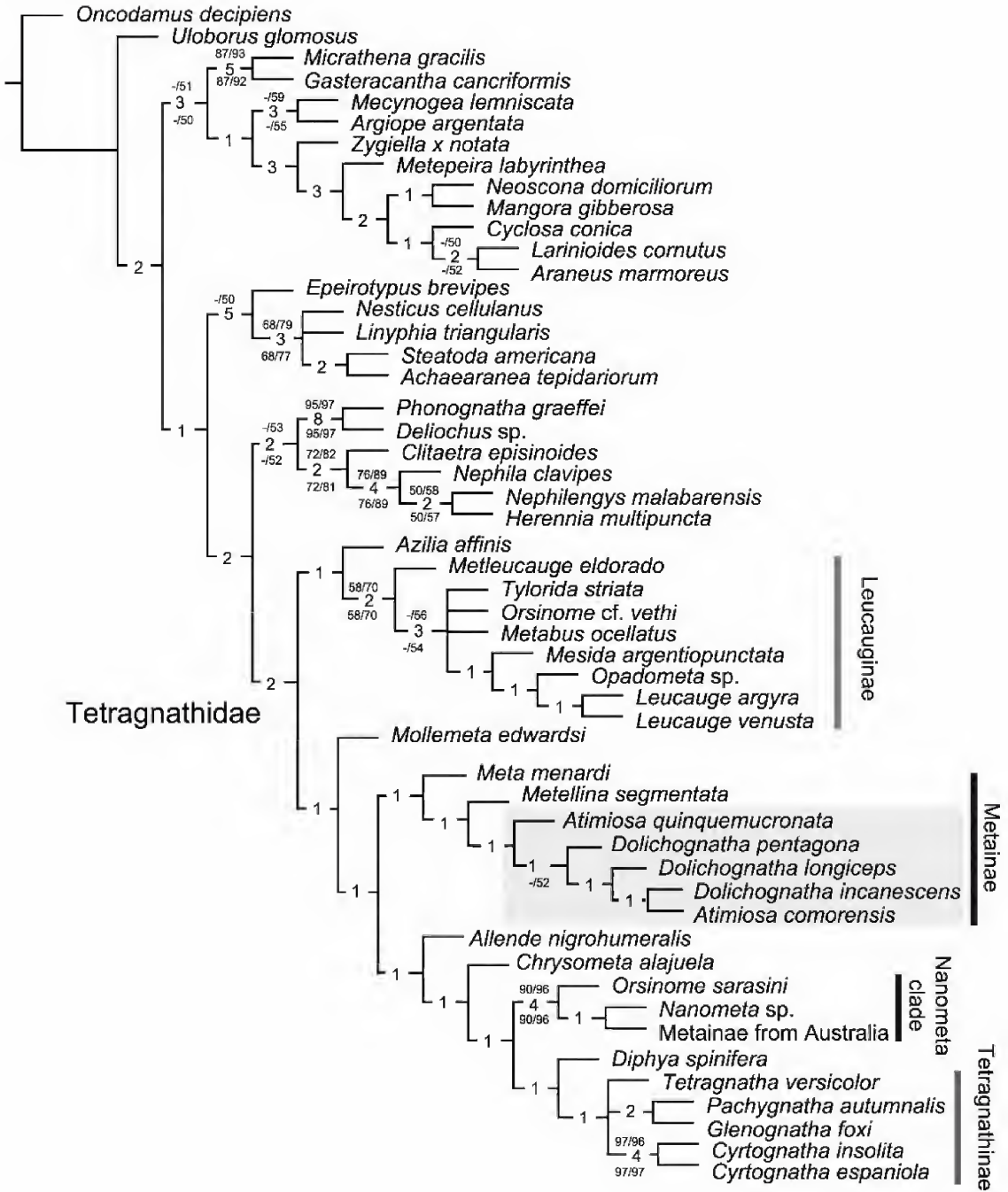


Fig. 9. Strict consensus of the six MPTs found by TNT under the equal weights parsimony criterion analyzing the complete data set (L = 1059, CI = 0.25, RI = 0.60). Numbers cutting the branches represent Bremer support; over the branches, standard bootstrap/jackknife; below the branches, Poisson bootstrap/symmetric resampling. *Dolichognatha* is shown in a gray box.

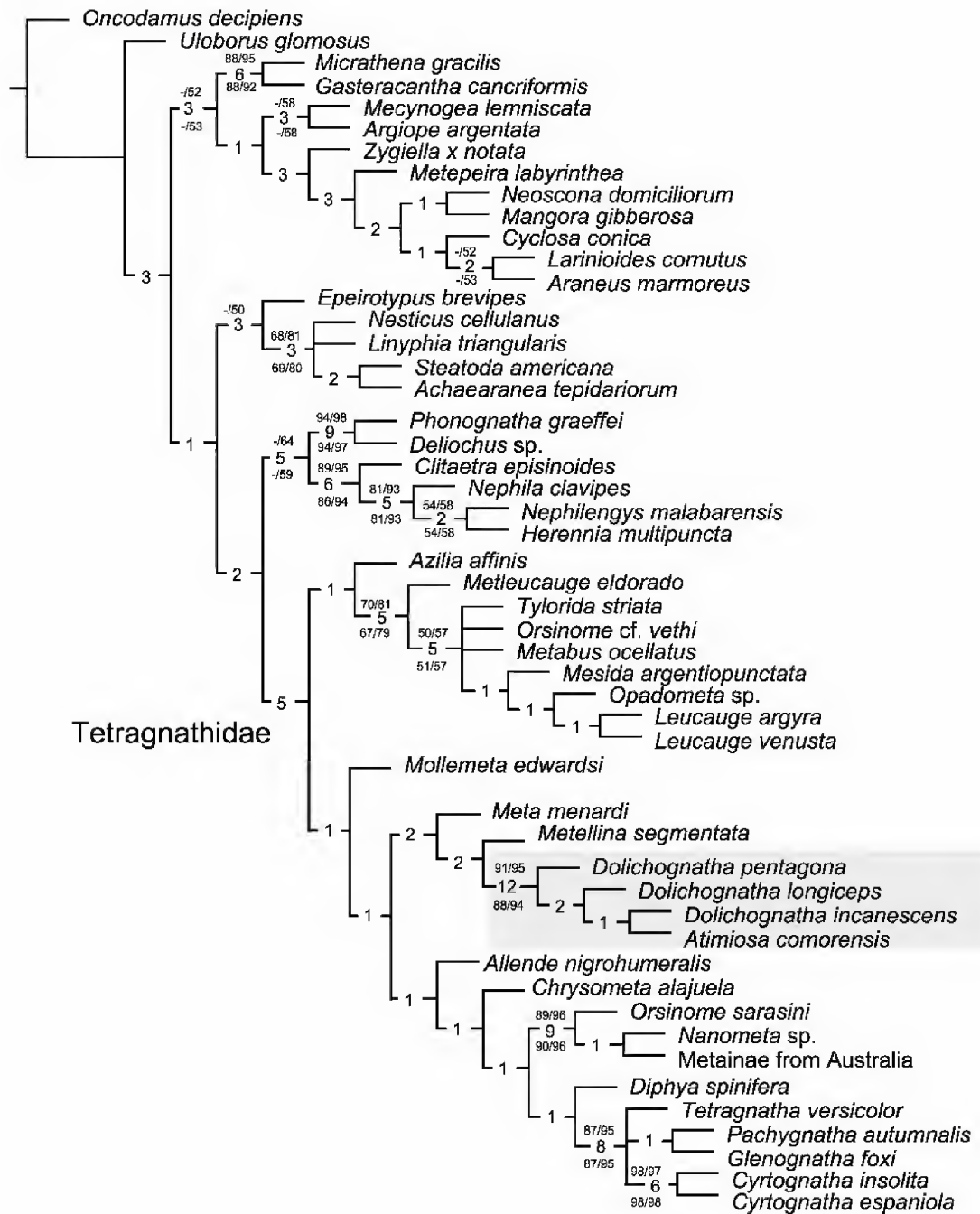


Fig. 10. Strict consensus of the six MPTs found by TNT under the equal weights parsimony criterion analyzing the matrix without *A. quinquemucronata* (L = 1058, CI = 0.25, RI = 0.60). Numbers cutting the branches represent Bremer support; over the branches, standard bootstrap/jackknife; below the branches, Poisson bootstrap/symmetric resampling. *Dolichognatha* is shown in a gray box.

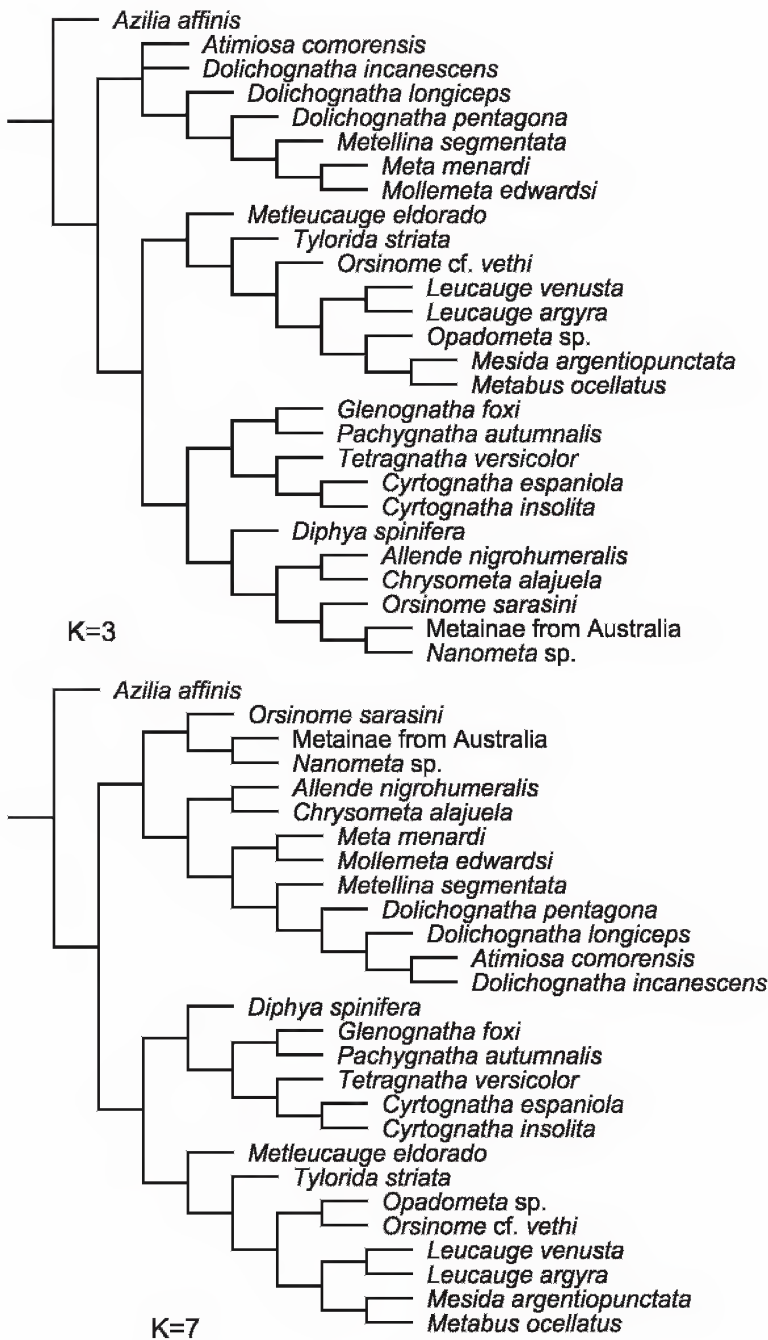


Fig. 11. Alternative topologies (above and at right, on opposite page) obtained analyzing the data under the implied weighting criterion using different values of the concavity constant k (*A. quinquemucronata* not included in the analyses).

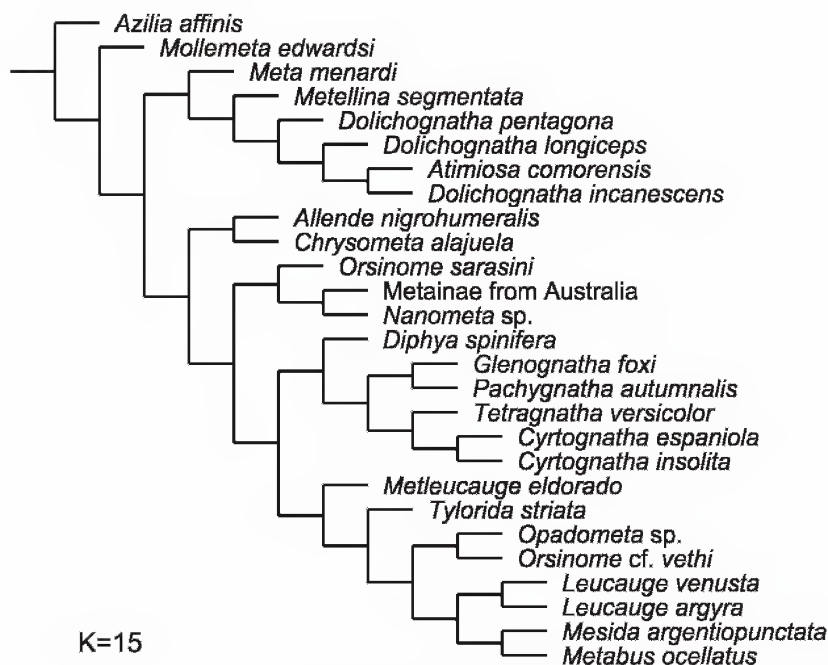


Fig. 11. Continued.

COMMENTS: There are three other species of *Dolichognatha* besides *D. quinquemucronata* described from Sri Lanka: *D. incanescens*, *D. nietneri*, and *D. albida*. This makes a reconciliation of the subadult specimen of *D. quinquemucronata* a very difficult task. However, the presence of characteristic abdominal tubercles in *D. quinquemucronata*, which differ from those of the other three Sri Lankan species, and its eye pattern, may prove useful if adults with these traits are collected. At present, as the holotype of *D. quinquemucronata* is a subadult specimen that cannot be identified, we suggest that it should be treated as *nomen nudum*.

Dolichognatha comorensis (Schmidt and Krause, 1993), **new combination**

Figures 2A–E; 3A–C

Atimiosa comorensis Schmidt and Krause, 1993: 6; Schmidt and Krause, 1994: 5.

TYPE: Holotype male from Comoros Islands, Grande Comoro, Boboni, 27.xi.1983, elevation 600m, R. Jocqué leg. (RMCA 160.649, examined).

JUSTIFICATION FOR THE TRANSFER: Morphology of the male palp of this species (presence of CBEP and metine embolic apophysis; shape of conductor and embolus) as well as eye size and arrangement are consistent with placement in the genus *Dolichognatha*. Transfer is further supported by the results from our cladistic analyses: parsimony analyses under equal and implied weights always, except when $k \leq 3$, found *A. comorensis* nested within *Dolichognatha* (figs. 9, 10).

Dolichognatha longiceps (Thorell, 1895)

Figures 4A–F; 5A–D; 6A–D; 7; 8

Prolochus longiceps Thorell, 1895: 122; Simon, 1895b: 932, 1004.

TYPES: Syntypes of *Dolichognatha longiceps* are deposited in NRM. We did not directly examine the type specimens ourselves. However, to ensure correct determination we have compared our specimens to a digital photograph of the male holotype that was kindly made available by Torbjörn Kronestedt and Gunvi Lindberg, and to the drawings available in the literature.

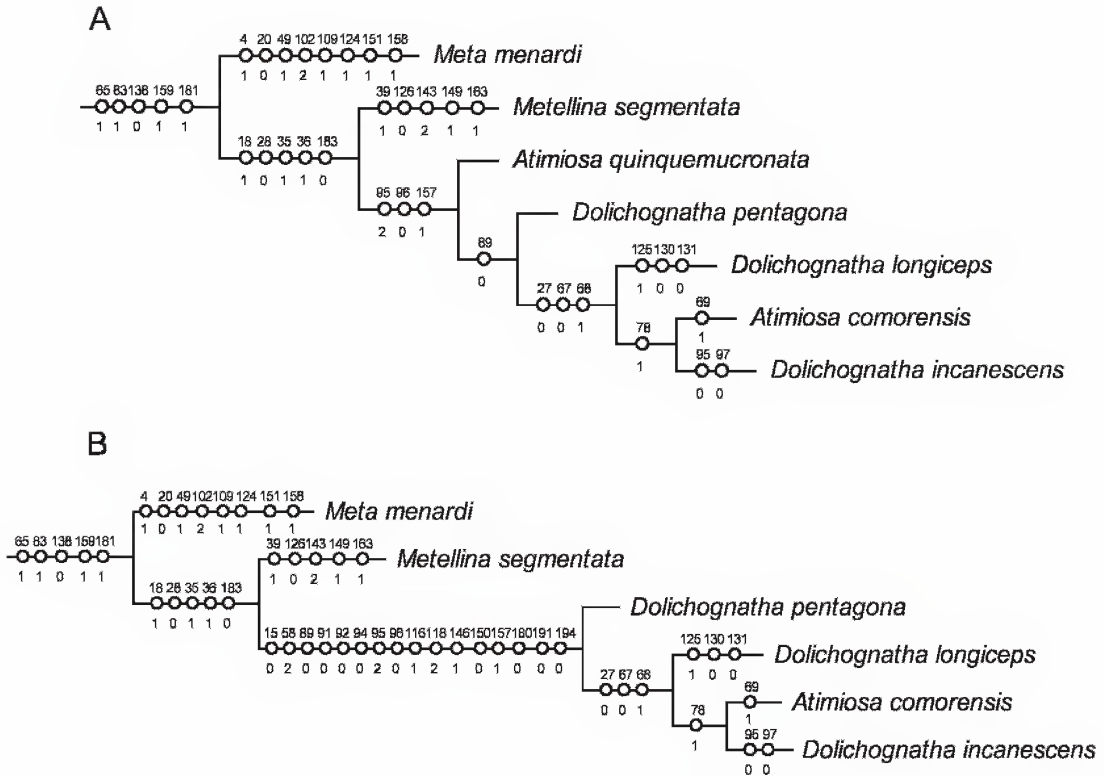


Fig. 12. Unambiguous synapomorphies of *Dolichognatha* and sister taxa mapped over the consensus tree from analyses of the complete matrix (A) and when *A. quinquemucronata* is not included in the analyses (B). All changes in the Metainae lineage depicted in this figure are homoplasious, thus marked with white circles.

DESCRIPTION OF THE WEB: *Dolichognatha longiceps* spins its orb web near the ground at the base of trees. The web that we observed was built between the buttresses of a tree. It is two-dimensional with oval shape (fig. 8A) and with a major axis of 40 cm. The web orientation is horizontal with dense spiral turns and numerous radii, without split radii (fig. 8). The web frame is an irregular polygonal shape and has numerous attachment sites (fig. 8A). The hub is closed (fig. 8B) and seems somewhat displaced toward one of the edges.

ADDITIONAL MATERIAL EXAMINED: One male and two females from Thale Ban National Park, Satun Province, THAILAND. N6° 42'37.0", E100°10'09.2", elev. 270m, 15–18.x. 2003, G. Hormiga leg. In AMNH.

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APPENDIX 1

MATRIX FOR CLADISTIC ANALYSES

Characters are numbered as in Álvarez-Padilla et al. (2009). Character descriptions and scores for the remaining taxa are discussed and published in Álvarez-Padilla et al. (2009).

Character																									
Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	
<i>Cyrtognatha insolita</i>	0	1	1	0	-	0	1	0	1	0	0	1	1	0	0	0	0	0	0	1	1	1	0	1	
<i>Dolichognatha longiceps</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Atimosa quinquemacronata</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Atimosa comorensis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Dolichognatha incanescens</i>	0	1	1	0	-	0	1	0	1	0	0	1	1	0	0	0	0	?	?	?	?	?	?	?	
	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	
<i>Cyrtognatha insolita</i>	1	0	-	0	-	-	0	-	-	0	1	0	1	1	1	1	1	0	0	1	1	0	0	0	
<i>Dolichognatha longiceps</i>	0	1	0	0	-	-	0	-	-	0	1	1	1	1	0	0	0	0	0	1	1	0	1	0	
<i>Atimosa quinquemacronata</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Atimosa comorensis</i>	0	1	0	0	-	-	0	-	-	0	1	1	1	1	0	0	0	0	0	1	1	0	1	0	
<i>Dolichognatha incanescens</i>	0	1	0	0	-	-	0	-	-	0	1	1	1	1	0	0	0	0	0	1	1	0	1	0	
	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	
<i>Cyrtognatha insolita</i>	0	0	0	-	1	0	0	0	1	2	1	0	0	1	1	1	0	0	2	1	2	0	0	0	
<i>Dolichognatha longiceps</i>	0	0	0	-	1	0	1	0	1	2	0	1	0	1	1	1	0	0	0	1	0	0	0	0	
<i>Atimosa quinquemacronata</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Atimosa comorensis</i>	0	0	0	-	1	0	1	0	1	2	0	1	0	1	1	1	1	0	0	1	1	0	0	0	
<i>Dolichognatha incanescens</i>	0	0	0	-	1	0	1	0	1	2	0	1	0	1	1	1	1	0	0	1	0	0	0	0	
	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	
<i>Cyrtognatha insolita</i>	0	0	0	1	0	-	0	1	1	2	0	0	0	0	1	0	0	0	1	1	0	1	1	1	
<i>Dolichognatha longiceps</i>	0	0	0	0	1	0	0	1	1	2	1	0	0	0	1	1	0	-	-	-	0	-	0	0	
<i>Atimosa quinquemacronata</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Atimosa comorensis</i>	0	0	0	0	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Dolichognatha incanescens</i>	0	0	0	0	1	1	0	1	?	2	1	0	?	?	?	?	?	?	?	?	?	?	?	?	
	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120	
<i>Cyrtognatha insolita</i>	1	0	0	?	1	0	0	1	1	0	0	2	0	1	1	0	1	0	2	0	1	2	0	0	
<i>Dolichognatha longiceps</i>	-	?	0	?	1	0	0	1	1	1	0	2	0	1	0	?	0	0	0	1	0	2	0	0	
<i>Atimosa quinquemacronata</i>	1	?	0	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Atimosa comorensis</i>	1	?	?	?	1	?	0	1	1	?	?	2	?	1	0	?	0	0	0	1	?	?	?	?	
<i>Dolichognatha incanescens</i>	0	?	0	?	1	?	0	1	1	?	?	2	?	1	0	?	?	?	?	?	?	?	?	?	

APPENDIX 1
(Continued)

Taxa	Character																							
	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140	141	142	143	144
<i>Cyrtognatha insolita</i>	0	0	0	-	-	-	-	-	-	2	1	0	1	1	-	-	-	-	-	1	0	-	2	0
<i>Dolichognatha longiceps</i>	0	0	1	0	1	1	0	-	-	0	0	0	0	0	0	0	0	0	0	?	?	?	?	0
<i>Atimiosa quinquemucronata</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Atimiosa comorensis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Dolichognatha incanescens</i>	0	0	1	0	0	?	0	-	-	1	1	0	0	0	0	0	0	0	0	?	?	?	?	0
	145	146	147	148	149	150	151	152	153	154	155	156	157	158	159	160	161	162	163	164	165	166	167	168
<i>Cyrtognatha insolita</i>	0	-	0	1	-	-	-	-	-	1	0	0	1	0	1	4	0	?	?	?	?	0	0	0
<i>Dolichognatha longiceps</i>	0	1	0	0	0	0	0	0	0	1	0	?	1	0	1	4	?	?	?	?	?	0	?	0
<i>Atimiosa quinquemucronata</i>	?	?	?	?	?	?	?	?	?	?	0	?	?	1	?	?	?	?	?	?	?	?	?	?
<i>Atimiosa comorensis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	0	?	0
<i>Dolichognatha incanescens</i>	0	1	?	0	0	0	0	0	?	?	0	?	1	0	?	?	?	?	?	?	?	0	?	?
	169	170	171	172	173	174	175	176	177	178	179	180	181	182	183	184	185	186	187	188	189	190	191	192
<i>Cyrtognatha insolita</i>	1	1	0	1	1	?	0	0	-	0	0	1	0	1	1	0	0	?	?	?	?	?	?	?
<i>Dolichognatha longiceps</i>	0	-	-	-	-	1	0	?	?	0	0	0	1	1	0	0	0	1	0	0	?	0	0	0
<i>Atimiosa quinquemucronata</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Atimiosa comorensis</i>	?	?	?	?	?	?	?	?	?	0	0	0	1	1	0	0	0	?	?	?	?	?	?	?
<i>Dolichognatha incanescens</i>	0	-	-	-	-	1	0	0	-	0	0	0	1	1	?	0	?	1	?	?	?	?	?	?
	193	194	195	196	197	198	199	200	201	202	203	204	205	206	207	208	209	210	211	212	213			
<i>Cyrtognatha insolita</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?			
<i>Dolichognatha longiceps</i>	?	0	?	0	?	0	0	0	?	0	0	1	0	?	?	?	?	?	?	0	?			
<i>Atimiosa quinquemucronata</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?			
<i>Atimiosa comorensis</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?			
<i>Dolichognatha incanescens</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?			